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LINKED QUANTITATIVE CHARACTERS IN WHEAT CROSSES

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SINCE wheat has but 8 chromosomes in the sexual cells and since the parents in the macaroni bread wheat crosses here discussed certainly differ in more than 8 visible characters, it was thought likely that a genetic linkage of some of these might be found. The following study is an endeavor to discover whether or not there is such a linkage between the shape of the head, *i. e.*, ratio of width of head (measured parallel to the face of the head which shows the sinuous furrow formed between the two rows of spikelets) to the thickness (measured parallel to the array of seeds in the spikelet) and the texture (translucency or opaqueness) of the grain. Of the two parents here discussed No. 1, the macaroni wheat, had a much flattened head and very hard translucent grains, whereas the other parent, No. 35 (a bread wheat), had a nearly square head with soft opaque grain.

The seed on the F_1 plants of this cross were all wrinkled and intermediate in texture between the two parents, *i. e.*, they were dull, being neither translucent like the macaroni parent nor opaque like those of the bread wheat parent. In order to make a quantitative expression of hardness the perfectly translucent grains of the macaroni parent were called 100 per cent. hard, the seeds of the F_1 50 per cent. hard and those of the bread wheat parent were called 0 per cent. hard. Since in the seeds of the F_2 and F_3 plants every possible degree of intergradation occurred between the characters of the two parents and since any form of classification adopted would be purely arbitrary, it was decided to make it the most simple possible and place all of the variants into three groups by the following means: a grain that was approximately as hard

TABLE I. CORRELATION BETWEEN $\left\{\frac{\text{WIDTH}}{\text{THICKNESS}}\right\}$ OF HEAD AND TEXTURE OF GRAINS. 1914

Ratio	$\left\{\frac{\text{Width}}{\text{Thickness}}\right\}$ of Head .60 .69	.70 .79	.80 .89	.90 .99	1.00 1.09	1.10 1.19	1.20 1.29	1.30 1.39	1.40 1.49	1.50 1.59	1.60 1.69	1.70 1.79	1.80 1.89	1.90 1.99	2.00 2.09	Average $\frac{W.}{T.}$	Total No. Plants	Character of Grain
Pure No. 1							3	7	12	46	*34*	23	21		4	1.63	150	Hard
1 × 35 F_1						1	1	5	4	*9*	12	3	4			1.56	39	Intermediate
Pure No. 35	1	4	*3*	1	2	1										.88	12	Soft

TABLE II. CORRELATION BETWEEN $\left\{\frac{\text{WIDTH}}{\text{THICKNESS}}\right\}$ OF HEAD AND TEXTURE OF GRAINS. 1915

	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199	200 209	210 219	220 229	230 239	240 249	250 259	260 269	270 279	Average W./T.	Total No. Plants	Character of Grain
Pure No. 1				1		5	8	17	22	36	*55*	55	56	32	3	4	2	1						1.57	298	Hard
Pure No. 1				1	1	23	26	26	39	37	*58*	58	47	21	5	6	1	1		1				1.55	352	Intermediate
1 × 35 F_2			2	8	8	29	40	78	85	55	*100*	88	64	67	3	28	25	7	2	2	1		1	1.55	693	Hard
1 × 35 F_2	2	3	7	28	44	161	196	*204*	175	96	120	68	48	47	1	17	3	4	1	1				1.29	1,226	Intermediate
1 × 35 F_2		5	10	34	61	96	*52*	36	15	11	7	3	1	1										1.11	332	Soft
Pure No. 35		3	14	40	*55*	41	13																	.95	166	Soft

TABLE III. CORRELATION BETWEEN $\left\{\frac{\text{WIDTH}}{\text{THICKNESS}}\right\}$ OF HEAD AND TEXTURE OF GRAINS. 1916

	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199	200 209	210 219	220 229	230 239	240 249	250 259	260 269	270 279	Average W./T.	Total No. Plants	Character of Grain
Pure No. 1				3	1	14	17	20	36	*40*	65	34	20	2	1									1.45	253	Hard
						1	3	1	8	10	*20*	9	2	1										1.50	55	Intermediate
1 × 35 F_3			2	4	5	44	88	153	184	225	*475*	322	291	215	40	140	55	23	4	2	3			1.59	2,275	Hard
1 × 35 F_3			3	9	14	120	198	313	*206*	116	171	53	38	20	1	20	4	5						1.33	1,291	Intermediate
1 × 35 F_3			6	7	19	147	208	*338*	177	66	64	16	8	2		5								1.24	963	Soft
Pure No. 35	1	5	12	25	38	*71*	63	25			1													1.04	241	Soft

as the macaroni parent was called 100 per cent. hard; a grain as soft as the bread wheat parent was called 0 per cent. hard; all grains intermediate between these were called 50 per cent. hard. A plant which produced 60 per cent. hard grains, 30 per cent. intermediate grains and 10 per cent. soft grains would therefore be classified as follows:

$$.60 \times 1.00 + .30 \times .50 + .10 \times 0 = .75 = 75 \text{ per cent. hard.}$$

Spotted grains (grains containing well-defined areas of opaque starch in an otherwise translucent grain) such as occur frequently in the macaroni wheat and also among the hybrids were treated as intermediate grains. After classifying the seeds of each plant in this manner all those which were over 66⅔ per cent. hard were termed hard wheats, those from 33⅓ to 66⅔ per cent. hard were classed as intermediate and all less than 33⅓ per cent. hard were classed as soft.

In 1914 the two parents (Nos. 1 and 35) and F_1 of this cross were grown with the following results:

The ratio, W./T. of the F_1 plants of this cross, is thus seen to be much nearer to the macaroni parent both in average and distribution than it is to the bread wheat parent.

Table II shows this same study made for the F_2 plants, grown in 1915.

A uniform correlation between the hardness of the grain and the ratio of width to thickness of head is apparent in Table II.

Table III gives the results of this same study for the crop of 1916. There is again apparent a marked correlation between the ratio of width to thickness of head and the texture of the grain. It will be noticed that both in 1915 and 1916 the soft (0 per cent. hard) hybrids had a higher average ratio W./T. than the sonora. It should, however, be remarked that the hybrid softs were also harder on the average than the pure number 35, but since

TABLE IV

DISTRIBUTION OF PLANTS WITH REGARD TO THEIR PERCENTAGE OF HARD GRAINS AND THE RATIO OF WIDTH TO THICKNESS OF HEAD

	Pure No. 1 in 1915											Pure No. 1 in 1916										
	Percentage of Hard Grains											Percentage of Hard Grains										
	100 96	95 91	90 86	85 81	80 76	75 71	70 66	65 61	60 56	55 51	50 46	100 96	95 91	90 86	85 81	80 76	75 71	70 66	65 61	60 56	55 51	50 46
244 240	1																					
239 235																						
234 230																						
229 225								1														
224 220						1																
219 215																						
214 210			1		1				1													
209 205																						
204 200	1	1		1	1			2	1	1	2											
199 195																						
194 190	1		1		1			2	2	1			1									
189 185	5		1	2	2	3	1	3	6	2	1											
184 180	1	2	4	3	1	4	3	2	4	3		2							1			
179 175	3	2	4	1	7	5	4	6	9	8	1											
174 170	3	2	5	3	3	8	6	10	10	4	1	10	3	3	2	1	1			2		
169 165	3	2	2	3	1	1	1	4	2	12	4	4		2		1		1				
164 160	6	2	7	4	6	9	8	9	11	10		11	1	5	3	5	2	5	1	1	1	
159 155	6	4	2	4	3	4	8	10	1	9	3	8	2	2			1		1			
154 150	3	3	5	4	3	2	4	6	11	14	4	25	4	7	5	5	6	4	7	4	4	
149 145	2	5	2	1	4	5	6	3	4	10	3	6	2	3	1	1			1			
144 140	1	1		1	2	4	2	3	2	4	8	11	9	5		1	1	3	4		1	1

	Pure No. 1 in 1915											Pure No. 1 in 1916										
	Percentage of Hard Grains											Percentage of Hard Grains										
	100 96	95 91	90 86	85 81	80 76	75 71	70 66	65 61	60 56	55 51	50 46	100 96	95 91	90 86	85 81	80 76	75 71	70 66	65 61	60 56	55 51	50 46
139 135	3	2		2	1	2	2	4	5	7	7	13	4	1	1	2			2	2	1	
134 130	1	1	1	3		2	2	3	3	8	2	5	4	1	2	1	2	2	1			
129 125		2	1	3		2	3	1	4	11	8	11	1	3	1		1					
124 120	1		1		1		1			1	1	5	1	1					1			
119 115		1	2	2	1	1	1	2	3	16	5	12	3		1				1			1
114 110												1						1				
109 105				1		2		1	2	9	5	4		1								
104 100				1	1					2	4	5	3			1		1				
99 95																						
94 90											1	1										
89 85												1										
84 80		1								1					2							

they were opaque and graded insensibly into the condition of pure No. 35 it was considered impracticable to make the arbitrary designation of degrees of hardness any more complex than the three groups used. It should be added, on the other hand, that a number of races were secured which were as soft or softer than the type of No. 35 and a number of races which, to all appearances, were fully as hard as pure No. 1. The inheritance of hardness will, however, be reserved for discussion in a later paper.

The question now arises as to whether this correlation is genetic or physiological. Might it not be caused by the simple fact that poorly filled (with starch) hard grains will give rise to a more flattened head, than will plump (starchy, soft) grains by failing to fill up and distend the glumes? This question can be answered by studying the correlation between the flattening of head and hardness of grain in a pure race. Since all of the No. 35 was soft, this study could not be made for the soft wheat, but as there were many plants of the pure macaroni which produced a greater or less proportion of soft grains, a comparison was possible. That the plants producing a large proportion of hard grains on an average did not have more flattened heads than those which produced a greater proportion of soft grains is shown in Tables II and III by comparing the "hard" with the "intermediate" groups of pure No. 1. This is perhaps better shown in Table IV, where the distribution of the plants is made with regard to their hardness per cent. and the ratio of width to thickness of head.

It should be noted from Tables II and III that there are numbers of individual plants with low ratios of width to thickness of head, but with high percentages of hard grains. It is difficult to see how this could occur if the low ratio was due simply to the lack of plumpness of the hard grain. *Moreover, races of hard macaroni wheats occur which have approximately square heads, and there are varieties of soft wheats* (*Little Club*) *with rather strongly flattened heads.* In 1916 there were a few cases where hybrid races having low average ratios (W./T.) also were rather high in average per cent. of hard grains. All of the races in 1916 having ratios averaging as low or lower than 1.35 and average percentages of 60 or more per cent. of hard grains are given in the following table:

It is thus seen that all of the races which on the average violated the correlation in 1916 came from plants which more or less markedly violated this same correlation in 1915. The cases given would indeed be hard to explain on a basis of violation of physiological correlations but if we are dealing with a genetic correlation, they may be easily explained on the "cross over" theory as used by Morgan for reversal of linkages in the characters of *Drosophila.*

TABLE V

INHERITANCE OF NON-CONFORMITY TO USUAL CORRELATION BETWEEN HIGH RATIO W./T. OF HEAD AND AVERAGE PERCENTAGE OF HARD GRAINS

No.	Parents in 1915		Offspring in 1916	
	W./T.	Per Cent H.	W./T.	Per Cent H.
132	.93	98	1.34	88
169	1.10	50	1.24	73
219	1.20	50	1.35	93
232	1.25	100	1.33	86
239	1.33	60	1.30	88
263	1.00	64	1.17	61
279	1.27	50	1.35	79

In the opposite direction, *i. e.*, races which markedly violated the correlation by having very high ratios (1.50 or more) but with low percentages of hard grains did not occur.

Again it may be objected that an explanation of this correlation between shape of head and texture of grain as a genetic linkage, is incorrect because the linkage is not complete, *i. e.*, there is considerable regression. This objection may be fully met by the observation that both of the characters here concerned are quantitative and hence subject to fluctuation around a mean. Moreover, it is almost certain that both characters are genetically compound, *i. e.*, each are the result of more than one factor, recombinations of which may markedly vary the quantitative visible expression of the characters. If, therefore, but a single factor for grain texture be linked with one of the factors concerned in the shaping of the head, there will result a partial correlation of these two characters such as we find.

The data here presented, therefore, seems to indicate that the two characters, hardness of grain and high ratio of width to thickness of head, which entered this cross together in the macaroni parent, tend to come out together in the segregates of the F_2 and F_3 generations, *i. e.*, that there is a genetic linkage between one or more of the factors controlling the grain texture and head shape in the two varieties employed as parents.